NOTES AND COMMENTS

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VIBRATIONAL SIGNALS ASSOCIATED WITH MATING BEHAVIOR IN THE TREEHOPPER, *ENCHENOPA BINOTATA* SAY (HEMIPTERA: HOMOPTERA: MEMBRACIDAE)

Enchenopa binotata Say is actually a complex of several species of arboreal treehoppers associated with six genera of trees in eastern North America (Wood and Guttman, 1981). Detailed life history and phylogenetic studies suggest that speciation in these treehoppers may have occurred in sympatry (Wood and Keese, 1990; Wood et al., 1990, and references therein). Egg hatch and development are tightly linked to host phenology and mating occurs between individuals that are similar in age. Thus, transfer to a new host with a different seasonal phenology within the same habitat could result in temporal reproductive isolation and genetic divergence. In addition to temporal isolation, *Enchenopa* occurring on different hosts are behaviorally isolated. Under experimental conditions, Wood and Guttman (1982) found that females mate preferentially with males originating from the female's host plant. Wood and Keese (1990) suggest that development of female preferences after divergence along host plant lines may be an important factor that enhances reproductive isolation. However, the mechanism by which females discriminate among males is unknown.

In some auchenorrhynchous Homoptera (e.g., leafhoppers and planthoppers), mating behavior is mediated by substrate-borne vibrational song (Claridge, 1985a, b). The study of inter- and intraspecific variation in leafhopper and planthopper song has proven useful in resolving taxonomic and systematics problems and in understanding the role of song in mate recognition, reproductive isolation, and mate choice (Claridge, 1990; Heady and Denno, 1991; De Winter, 1992; Hunt et al., 1992; Gillham, 1992). Much less is known, however, about intersexual communication in treehoppers. Recent studies of *Strictocephala bisonia* Kopp and Yonke (Strübing, 1992) and *Spissistilus festinus* (Say) (Hunt, 1993) demonstrated that mate recognition and attraction are mediated by vibrational communication. In the present study, *E. binotata* individuals were observed to determine whether vibrational signals are associated with mating behavior.

MATERIALS AND METHODS

Individual males, females, or precopulatory pairs (see Wood and Guttman, 1982) were collected from a mature redbud tree (*Cercis canadensis* L.) located in an urban landscape in Lexington, KY. Males and females were housed in separate cages containing potted redbud saplings for a period of 0.5–3 d before they were observed. Observations were done between July 28 and August 10, 1992. Voucher specimens were deposited in the University of Kentucky insect collection.

Individual males (N = 10), females (N = 10), or pairs of males and females (N =

15) were placed on the main stem of a potted redbud sapling and observed for one h. Vibrational signals were recorded by resting a phonograph cartridge (Model 39-160, MCM Electronics, Centerville, OH) on the stem 3–5 cm from an individual or pair. Signals were amplified 100-fold using a preamplifier (Model P-16, Grass Instr. Co., Quincy, MA) and recorded on a digital tape deck (Model DTC-700, Sony Corp., Sun Valley, CA) at 48,000 samples/s. Signals were monitored using headphones. Recorded signals were analyzed using a Macintosh computer equipped with Audiomedia (Digidesign, Menlo Park, CA), Alchemy (Passport Designs, Half Moon Bay, CA), and SoundScope (GW Instr., Somerville, MA) hardware and software. Temperature was maintained at 23° ± 2°C during observations. Although experimental approaches will be necessary to demonstrate that the vibrations documented in this study have a communicative function, I tentatively refer to these vibrations as signals, calls or songs.

RESULTS AND DISCUSSION

Individual males (8/10) emitted at least one spontaneous call during the observation period. Each of these calls was composed of two sections (Fig. 1). The first section consisted of an amplitude- and frequency-modulated wave train. The second section consisted of 2 to 10 pulses. Emission of calls was associated with abdominal quivering that was readily visible at a distance of ≤0.25 m. In addition to these complex calls, males occasionally emitted simple vibrations by striking the stem with their abdomen (not figured). These percussive signals were often emitted in doublets or triplets. Isolated females did not emit complex calls, but they did occasionally emit percussive signals similar to those emitted by males. Four of the 15 pairs of males and females mated and the series of behaviors prior to mating were similar for each pair. Each male that mated emitted at least one call of the type emitted by isolated males before climbing onto the side of the female (see Wood and Guttman, 1982). Each male then emitted a courtship song. A second courtship song was detected immediately before copulation. However, the amplitude of the second song was very low and the identity of individuals that produced these vibrations is not certain. The first courtship song consisted of repeating units each of which was composed of a repeating phrase, a single rumbling-like vibration, and a single wing flick (Fig. 2). The first portion of the repeating phrase consisted of a frequency-modulated vibration. The second portion of the phrase was a vibration that produced a pulsed, "rumbling-like" sound similar to the vibration at the end of a unit. After the phrase was repeated several times, the rumble portion of the phrase continued for several seconds, culminating in a wing flick. Repetition of the entire unit continued for several minutes before the emission of the second courtship song. The second song (not figured) consisted of two alternating vibrations that were frequency-modulated. In each case, the second song lasted less than 1 min and ended when genitalia joined.

In a study of *S. festinus,* Hunt (1993) provided experimental evidence that mate recognition and finding depend on the exchange of vibrational signals between males and females. Males of this species spontaneously emit a calling song. Females readily emit response calls in response to calling males located at distances of >60 cm. Vibrational exchanges continue while males search for stationary females. The overall structure of spontaneous calls emitted by *E. binotata* males is similar to that emitted

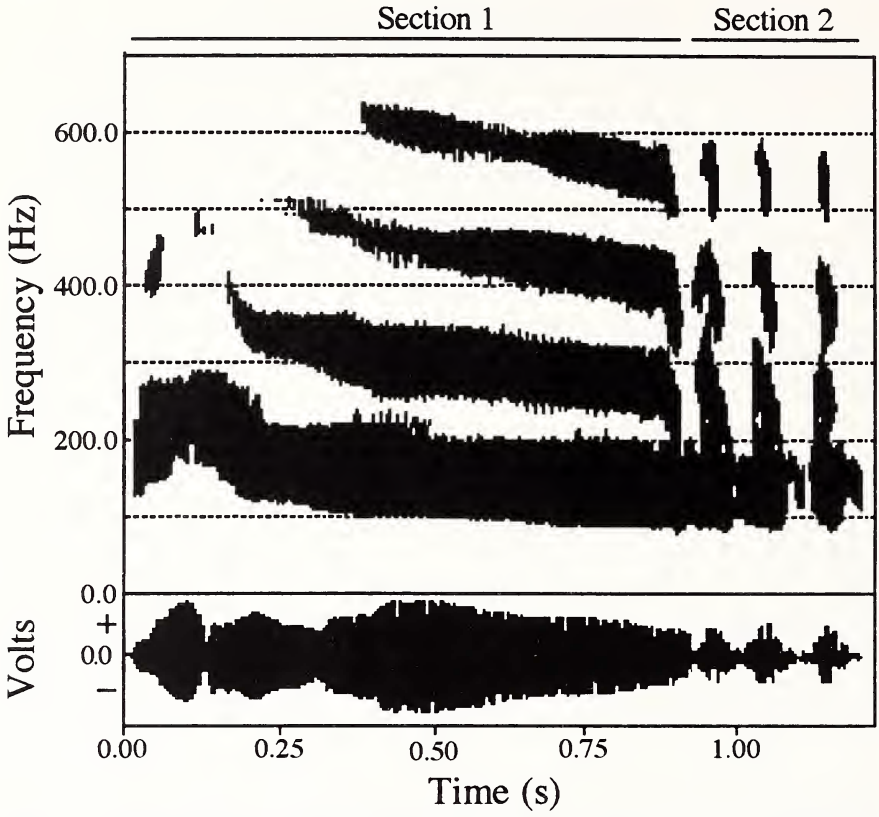

Fig. 1. Oscillograph (lower) and sonograph (upper) of a spontaneous call emitted by an isolated *Enchenopa binotata* male.

by *S. festinus* males. Although long-distance vibrational interactions and search behavior were not examined in the present study, it is possible that the spontaneous call and/or percussive signals emitted by isolated *E. binotata* males and percussive and/or other signals emitted by females might mediate long-distance communication.

Vibrational signals and accompanying male/female interactions displayed by *E. binotata* during courtship appear to be far more complex and ritualized than in *S. festinus*. In *S. festinus* songs emitted by males and females during courtship do not differ greatly from those emitted during initial exchanges and while males search. In contrast, courtship behavior in *E. binotata* involves the sequential emission of two highly structured songs, both of which are quite different than the spontaneous call emitted by males prior to courtship. Although correlation of abdominal movement to the production of vibrations suggests that males are the predominant singers during courtship, it is possible that some of these vibrations were produced by the females.

Future studies of *E. binotata* will employ experimental approaches to determine the role of vibrational signals in mate recognition, finding, and courtship. Also, the

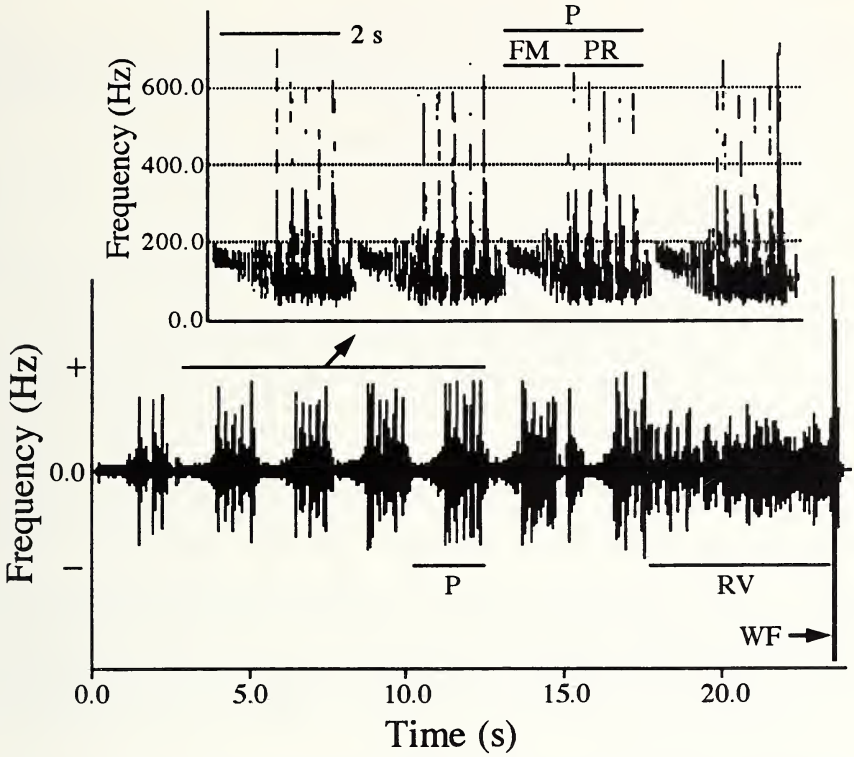

Fig. 2. Oscillograph (lower) showing a single unit of the first courtship song emitted by an *Enchenopa binotata* male. The unit is composed of repeated phrases (P), a rumbling-like vibration (RV), and a wing flick (WF). Sonograph (inset) of four repeated phrases expanded from the region indicated in the oscillograph. Each phrase (P) is composed of a frequency-modulated vibration (FM) and a pulsed "rumbling-like" vibration (PR).

study of inter- and intraspecific variation in vibrational signals produced by members of the *E. binotata* complex and determination of whether female preference is based on evaluation of male vibrational signals may provide insights into speciation and the basis of premating reproductive isolation in these treehoppers.—*Randy E. Hunt, Department of Entomology, University of Kentucky, Lexington, Kentucky 40546–0091.*

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STRIDULATORY MECHANISMS IN AQUATIC AND SEMIAQUATIC HETEROPTERA

A number of new discoveries of putative stridulatory mechanisms in aquatic and semiaquatic Heteroptera are reported here, and previously recognized structures